These are followed by other strands below the scion almost in continuity with those of the uncut ends. Strands also appear in the callus near the lower edges of the cuticle-covered epidermis of the ends. Later, more strands appear in the callus on the flanks, even farther out and lower down than those reported above (TEXT-FIG. 2). At the time that experiments were stopped — and a 54-day period was the longest any were maintained in culture — the strands were all of short vertical extent. Their ultimate length and possible duration of development are unknown.

It is important to realize that vascular strands in the positions which many of these occupy and with no more continuity than they exhibit could have little significance as water-conducting xylem. One cannot avoid pondering this fact in terms of the pattern of development in normal stems. Is the solution of this problem of the differentiation of xylem in the cylindrical or near-conical axis of the shoot to be found in the fact that continuing strands of elongating procambial cells are preferred paths for auxin movement? If carbohydrates carried by phloem represent a second necessity for xylem differentiation, then one can recognize the significance of the characteristic pattern of phloem differentiation preceding xylem differentiation at any level (Jacobs, 1954). Given carbohydrate, through differentiated phloem elements, and auxin in adequate amounts, it appears that these factors are no longer limiting to xylem differentiation. As it is likely that the favorable concentrations of auxin and carbohydrate are likely to be in the procambium, it is to be expected that xylem formation should be associated with the presence of phloem.

Importance is attached to the fact that vascular strands can experimentally be somewhat generally allocated to regions of the callus. If, instead of a 1% agar as the medium to fill the cut before the scion is inserted, the agar contains a synthetic auxin in known concentration in the physiological range, the vascular strands formed in the callus reflect the auxin concentration. With a concentration of 1 mg. per l., the strands occur only towards the outside of the callus, very few being found near the scion. With 0.01 mg. per l. in the agar placed in the incision, few strands occur near the periphery of the callus — in pieces approximately 1 cm. on a side; they tend to be aggregated on the lower flanks and below the scion. In a broad way, the number and distribution of the strands is dependent upon the concentration of the auxin, at least for either naphthaleneacetic acid or indole-3-acetic acid, the only auxins tried.

When the usual V-shaped cuts are made in the callus, these cuts filled with an auxin-agar mixture, but no apex inserted, results are obtained not dissimilar to those with the apices. A low concentration of auxin (FIG. 21 with 0.25% n.a.a. in lanolin) gives in four and a half months no strands at all. By contrast a medium containing 0.05 mg. per l. of n.a.a. + 15% autoclaved coconut milk, with its high concentration of indole-3-acetic acid, and 5% sucrose (FIG. 19) produces strands scattered in the callus. Few to none of these, however, are found in proximity to the cut, even though the auxin-agar was only replaced once during five and a third months. Again, when 5 mg. per l. of n.a.a. in 1% agar is put into the

incision, a cambial-like zone, very often found in similar cases, is produced toward the outside of the callus, which then resolves itself into strands of xylem, as can be seen (near the upper left, FIG. 20).

In summary, it seems clear that the findings from the early and beautifully planned experiments of Camus (1949) and the more recent and equally significant studies of Sinnott and Bloch (1944) and of Jacobs (1952, 1954) are further supported by the present investigations. It is clear that an auxin placed in or near the top of a callus can make the difference between the formation and the non-formation of vascular strands in which at least xylem differentiates. The role of sugar, as suggested by Jacobs, is not absolutely confirmed, though circumstantial evidence points to its probability. An important problem remains. Why do physiological concentrations of auxin in the agar medium foster the growth of *Syringa* callus *in vitro* but are not effective in the formation of vascular strands in the callus? Yet the same concentrations used in incisions on the upper surface of the agar are accompanied by the appearance of strands. This would seem to suggest a polarity to the callus, as was reported by Gautheret (1940) for carrot tissues, even when isolated from the carrot, and (1941) for endive root tissues. The general handling of callus tissues after a few transfers suggests little polarity, as indicated by a preferential absorption of auxin from the medium. One reasons thus from the fact that growth appears very uniform in pieces planted with little or no regard to their orientation with relation to the original plant. Experiments will be made to investigate the question of polarity of lilac callus in its relation to auxin transfer when initially grown and after varying numbers of passages to new media.

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LITERATURE CITED

BALL, E. 1946. Development in sterile culture of stem tips and subjacent regions of Tropaeolum majus L. and of Lupinus albus L. Amer. Jour. Bot. **33**: 301–318.

———. 1948. Differentiation in the primary shoots of Lupinus and Tropaeolum. Symposia Soc. Exper. Biol., II. Growth **1948**: 246–262.

———. 1949. The shoot apex and normal plant of Lupinus albus L., bases for experimental morphology. Amer. Jour. Bot. **36**: 440–454.

———. 1951. The influence of shoot apex on subjacent shoots of Lupinus albus L. Nature **167**: 16–18.

———. 1952a. Experimental division of the shoot apex of Lupinus albus L. Growth **16**: 151–174.

———. 1952b. Morphogenesis of shoots after isolation of the shoot apex of Lupinus albus. Amer. Jour. Bot. **39**: 167–191.

CAMUS, G. 1949. Recherches sur le rôle des bourgeons dans les phenomènones de morphogénèse. Revue de Cytol. et de Biol. Vég. **11**: 1–199.

CHEADLE, V. I., E. M. GIFFORD AND K. ESAU. 1953. A staining combination for phloem and contiguous tissues. Stain Tech. **28:** 49–53.

GAUTHERET, R. J. 1942. Manuel technique de culture des tissus végétaux. Masson et Cie, Paris.

JACOBS, W. P. 1947. The effect of some growth-hormones on the differentiation of xylem around a wound. Amer. Jour. Bot. **34:** 600.

———. 1952. The role of auxin in differentiation of xylem around a wound. Amer. Jour. Bot. **39:** 301–309.

———. 1954. Acropetal auxin transport and xylem regeneration — a quantitative study. Amer. Nat. **88:** 327–337.

JOST, L. 1940. Zur Physiologie der Gefässbildung. Zeitschr. Bot. **35:** 114–150.

———. 1942. Uber Gefässbrucken. Zeitschr. Bot. **38:** 161–215.

KAAN-ALBEST, ANITA VON. 1934. Anatomische und physiologische Untersuchungen über die Entstehung von Siebröhrenverbindungen. Zeitschr. Bot. **27:** 1–92.

MOREL, G. 1948. Recherches sur la culture associée de parasites obligatoires et de tissus végétaux. Ann. Epiphyties **14:** 1–112.

NITSCH, J. P. 1951. Growth and development in vitro of excised ovaries. Amer. Jour. Bot. **38:** 566–577.

———. 1955. The separation of natural plant growth substances by paper chromatography. Beitr. zur Biol. d. Pflanzen **31:** 387–408.

SIMON, S. 1930. Transplantationsversuche zwischen Solanum melongena und Iresine Lindeni. Jahrb. Wiss. Bot. **72:** 137–160.

SINNOTT, E. W. AND R. BLOCH. 1944. Visible expression of cytoplasmic pattern in the differentiation of xylem strands. Proc. Nat. Acad. Sci. **30:** 388–392.

WARDLAW, C. W. 1944. Experimental and analytical studies of Pteridophytes. III. Stelar morphology: the initial differentiation of vascular tissue. Ann. Bot. **8:** 173–188.

———. 1947. Experimental investigations of the shoot apex of Dryopteris aristata Druce. Phil. Trans. Roy. Soc. London **232 B:** 343–384.

———. 1949. Further experimental observations on the shoot apex of Dryopteris aristata Druce. Phil. Trans. Roy. Soc. London **233 B:** 415–451.

———. 1950. The comparative investigation of apices of vascular plants by experimental methods. Phil. Trans. Roy. Soc. London **234 B:** 583–604.

———. 1952. The effect of isolating the apical meristem in Echinopsis, Nuphar, Gunnera, and Phaseolus. Phytomorphology **2:** 240–242.

WETMORE, R. H. AND C. W. WARDLAW. 1951. Experimental morphogenesis in vascular plants.. Ann. Rev. of Plant Physiol. **2:** 269–292.

EXPLANATION OF PLATES

PLATE I

FIG. 1. Habit of *Syringa* apex grafted into *Syringa* callus, 7 weeks old. Graft incision filled with agar containing 2% sucrose and 0.1 mg./l. n.a.a.

FIG. 2. Habit of 19-week, 5-day-old graft of *Syringa* apex into *Syringa* callus. Agar mixture used in graft incision as above.

FIG. 3. Habit of 8.5-months graft of *Syringa* apex into *Syringa* callus. The graft was planted on the medium of FIGS. 1 and 2; at the end of 6 months it appeared about as in FIG. 2. Upon transfer to a medium containing 20% autoclaved coconut milk, casein hydrolysate (1%), it grew to the pictured, internode-bearing plant, rooted (see 2 short roots on right-hand plant) in about 2½ months. Note control apex in the middle, not grafted.

PLATE II

FIG. 4. Longitudinal section of callus-graft union of 5-weeks-old graft. Note black-stained agar around the base of the scion. Two lobes of the scion are shown on the left, the upper cut almost in median plane, the lower not shown in direct connection with the main body of the base of the scion. × 10.

FIG. 5. Transverse section of scion-graft union of a 54-day graft grown on a dextrose, yeast-extract medium with thiamin and cysteine, but no coconut milk nor synthetic auxin; 1% agar used in the incision. Section almost 1.5 mm. below surface of callus-graft union. Note upper and lower flanks of scion are along cut edges of wedge-shaped scion base. The side surfaces of the scion are epidermis-covered. × 11.6. (This section is about 500 μ below FIG. 6, but through an error was mounted out of order. The section labelled FIG. 6 and there described is actually FIG. 5 and that described as FIG. 5 is FIG. 6.)

FIG. 6. Transverse section about 500 μ above FIG. 5. Note increased diameter of vascular cylinder, due to radial multiplication of pith cells (See FIG. 13). × 11.6.

PLATE III

FIG. 7. Transverse section about 300 μ below FIG. 6. Note the arc of the vascular cylinder on the right is disrupted; radial organization of the pith is especially prominent on the left. Note the extra vascular strands on both flanks, above and below. See FIGS. 14, 15 for enlargements from section close to this one. × 11.6.

FIG. 8. Transverse section about 500 μ below FIG. 7. Note the narrowed wedge of the scion; two strands of vascular tissue are left, much decreased in size. Agar is irregularly distributed. As epidermis disappears on right, note appearance of strands in callus. See FIG. 16 for enlargement. × 11.6.

FIG. 9. Transverse section about 150 μ below FIG. 8. The left vascular strand of scion has disappeared, the right, almost so. A small black agar-contained area with remains of right vascular strand is obvious. Some strands are visible in the callus. × 11.6.

PLATE IV

FIG. 10. Transverse section over 0.5 mm. below FIG. 9. Right-hand arc of cylinder has disappeared, but it has been replaced by another almost below it. See TEXT-FIG. 2. Strands in the callus are more pronounced. × 11.6.

FIG. 11. Transverse section about 0.25 mm. below FIG. 10. Note continuing central strand and enlarged strands in the callus. × 11.6.

FIG. 12. Transverse section about 1.0 mm. below FIG. 11. Note increasing prominence of the numerous strands. × 11.6.

PLATE V

FIG. 13. Enlarged view of scion of FIG. 5. Note rows of new cells in pith on both sides; these radial rows have become extensive enough to displace laterally the original vascular tissue, tearing the pith and cortex of the scion and the adjacent callus. × 55.

FIG. 14. Enlarged view of scion of section 40 μ above FIG. 7. Note radial rows on either side of tear in pith. × 55.

FIG. 15. Enlarged view of right-hand part of vascular cylinder of FIG. 14. Note oblique vascular elements in upper part of radial rows; element marked X shows vessel perforation; neighboring elements in side view show crowded, circular bordered pits. × 67.

FIG. 16. Enlarged view of scion from section 50 μ above FIG. 8. Note reduction of arcs of vascular cylinder; radial rows and tears in pith still obvious. × 50.

FIG. 17. Enlarged view of much smaller scion 20 μ below FIG. 8. Note rapid reduction in extent of vascular strands in the 70 μ between FIG. 16 and FIG. 17. Radial organization of pith still present. Note limits of grafted scion as indicated by black agar lines. × 50.

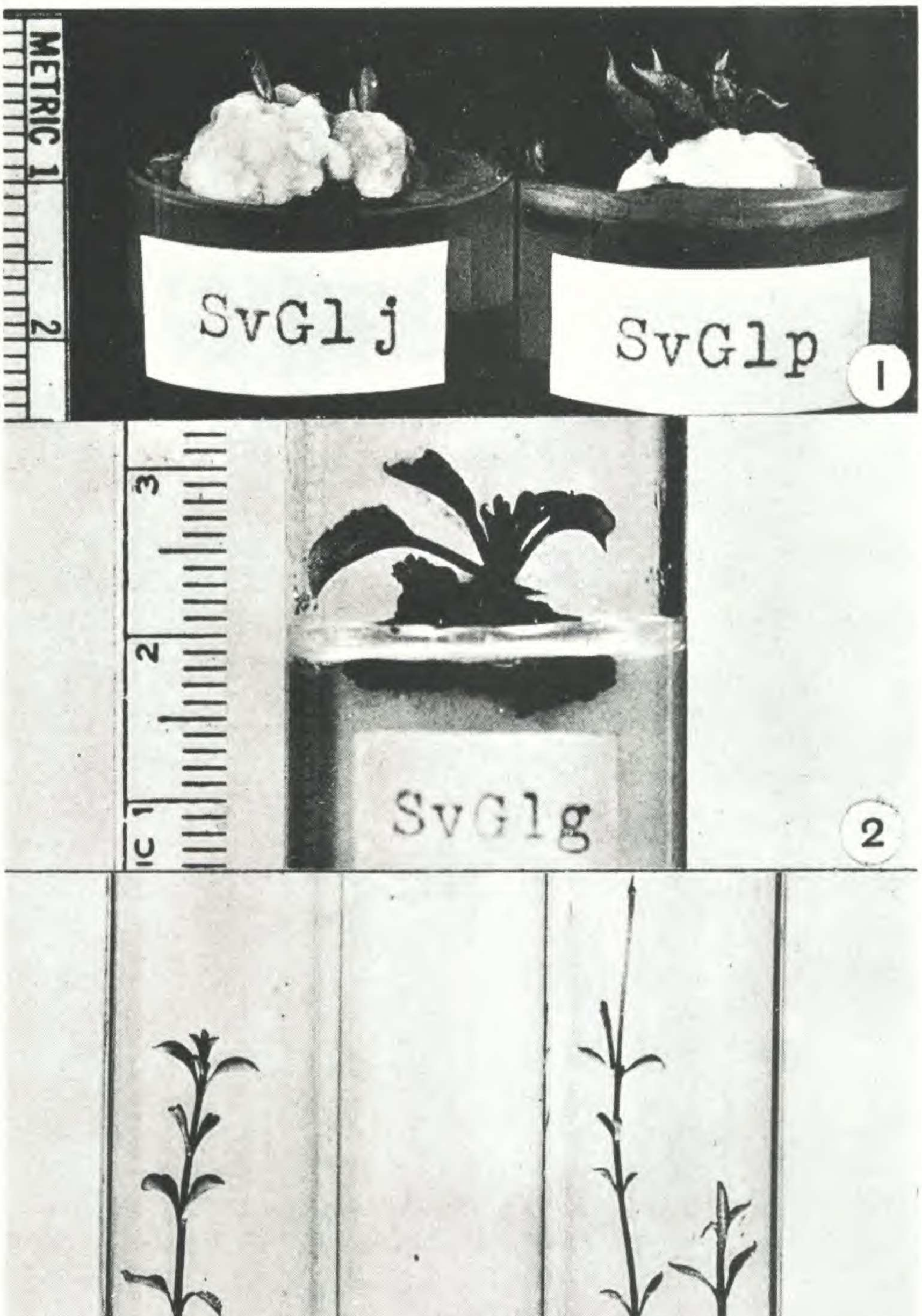
FIG. 18. Enlarged view of transverse section of scion 90 μ below FIG. 17 (or 40 μ above FIG. 9). Note left-hand strand has disappeared leaving the large proliferated parenchymatous mass at base of scion. The right-hand strand is present, circular in outline. × 45.

PLATE VI

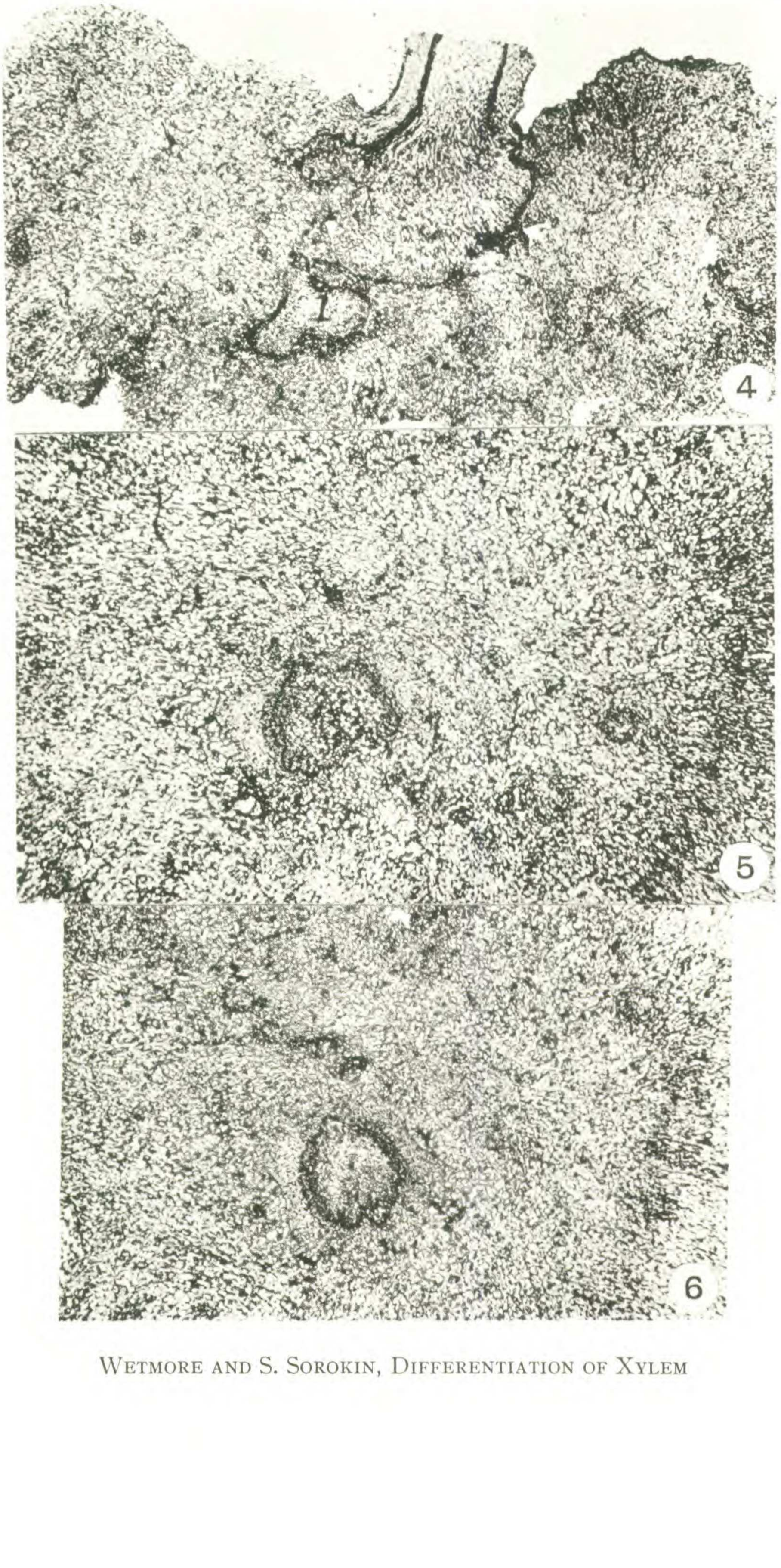
FIG. 19. Transverse section of callus cut through remains of V-shaped cut after 5 1/3 months. Cell proliferation has almost filled the incision, only irregular bits remaining. Little of the agar is visible, though it was replaced once. The agar contained 15% coconut milk and 5% sucrose. Note extensive cell proliferation midway out in callus which has given way to vascular tissue. × 4.2.

FIG. 20. Transverse section of 31-day callus after incision in upper surface was filled with agar containing n.a.a. in a concentration of 5 mg. per l. and 5% sucrose. Mixture replaced once. Note absence of vascular strands near incision, and the rectangular cambial-like layer near the periphery. This layer begins to show strands in the upper left. × 10.4.

FIG. 21. Transverse section of a 4½-months' callus grown on a favorable medium with an incision in the top filled with 0.25% n.a.a. in lanolin which was replaced once. Note the absence of vascular strands over the whole callus; auxin diffuses much more slowly from lanolin than from auxin.



WETMORE AND S. SOROKIN, DIFFERENTIATION OF XYLEM



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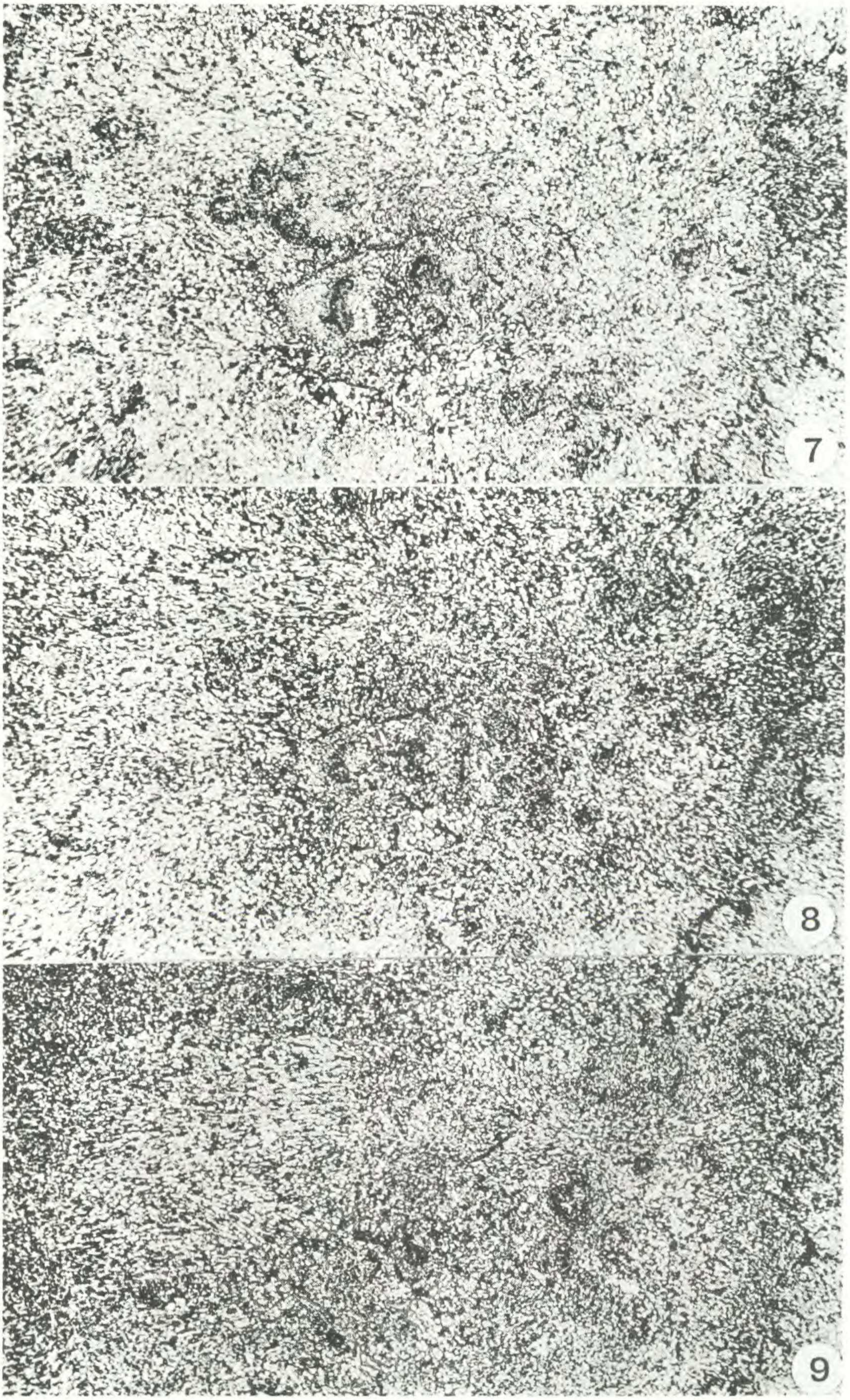

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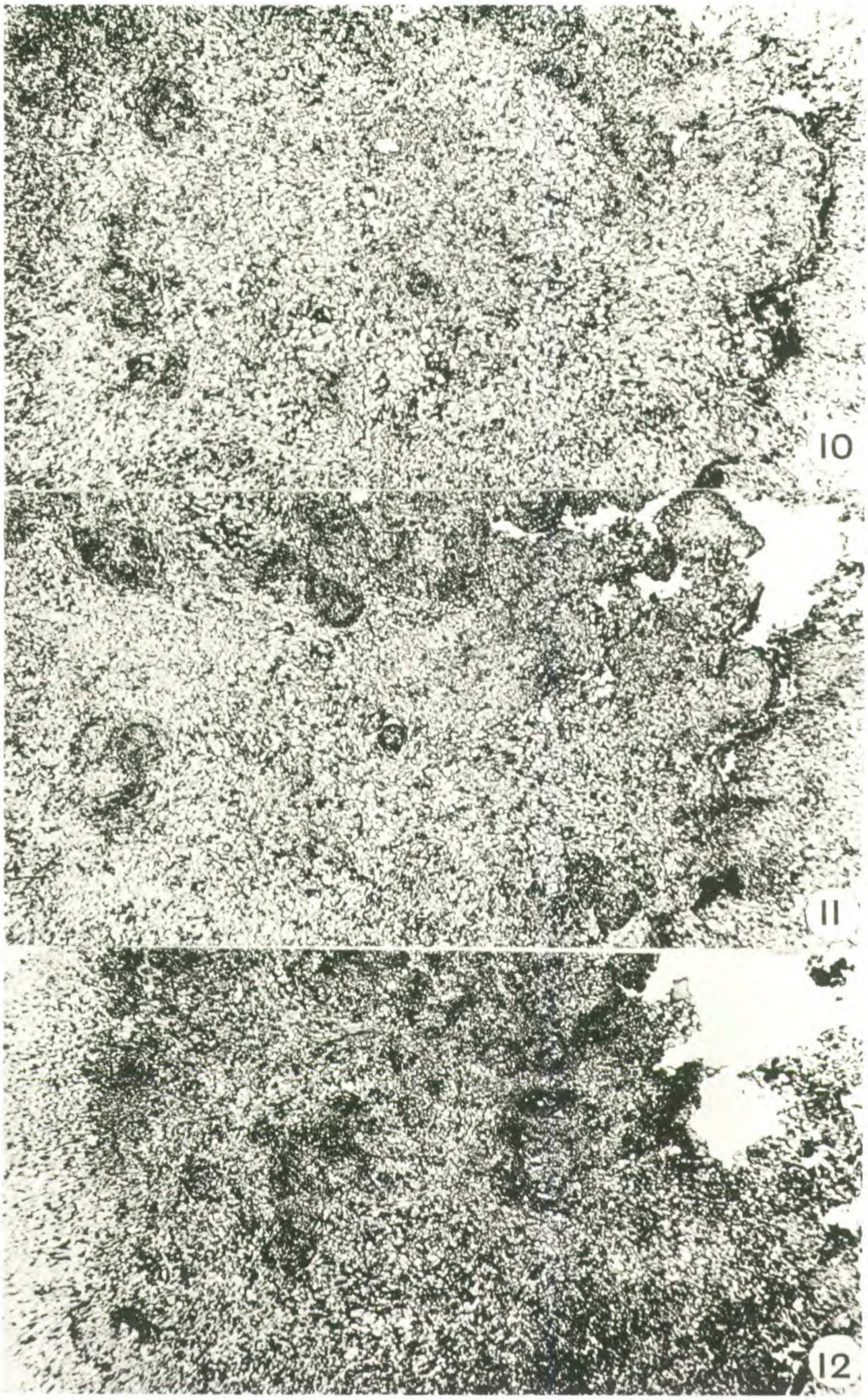

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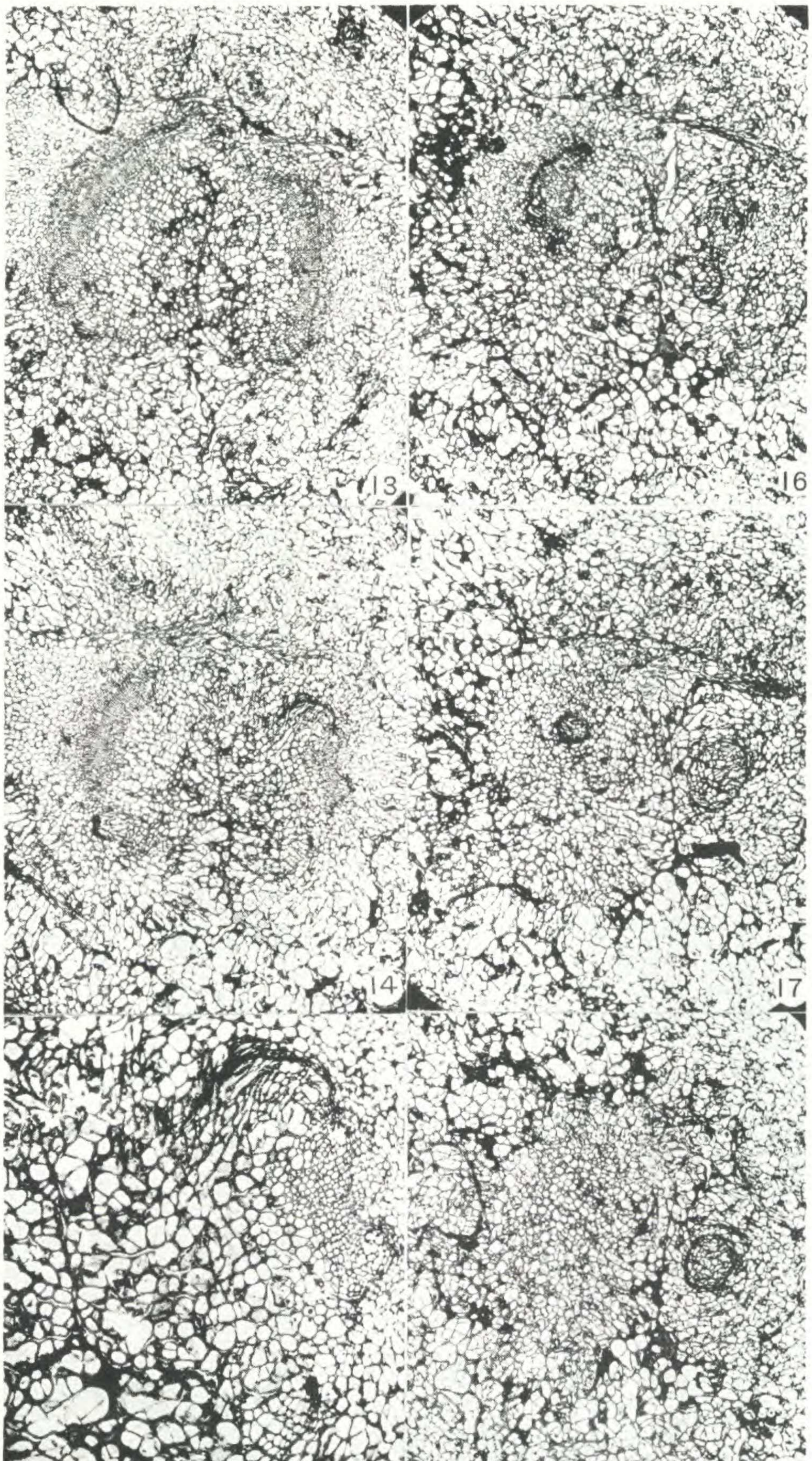

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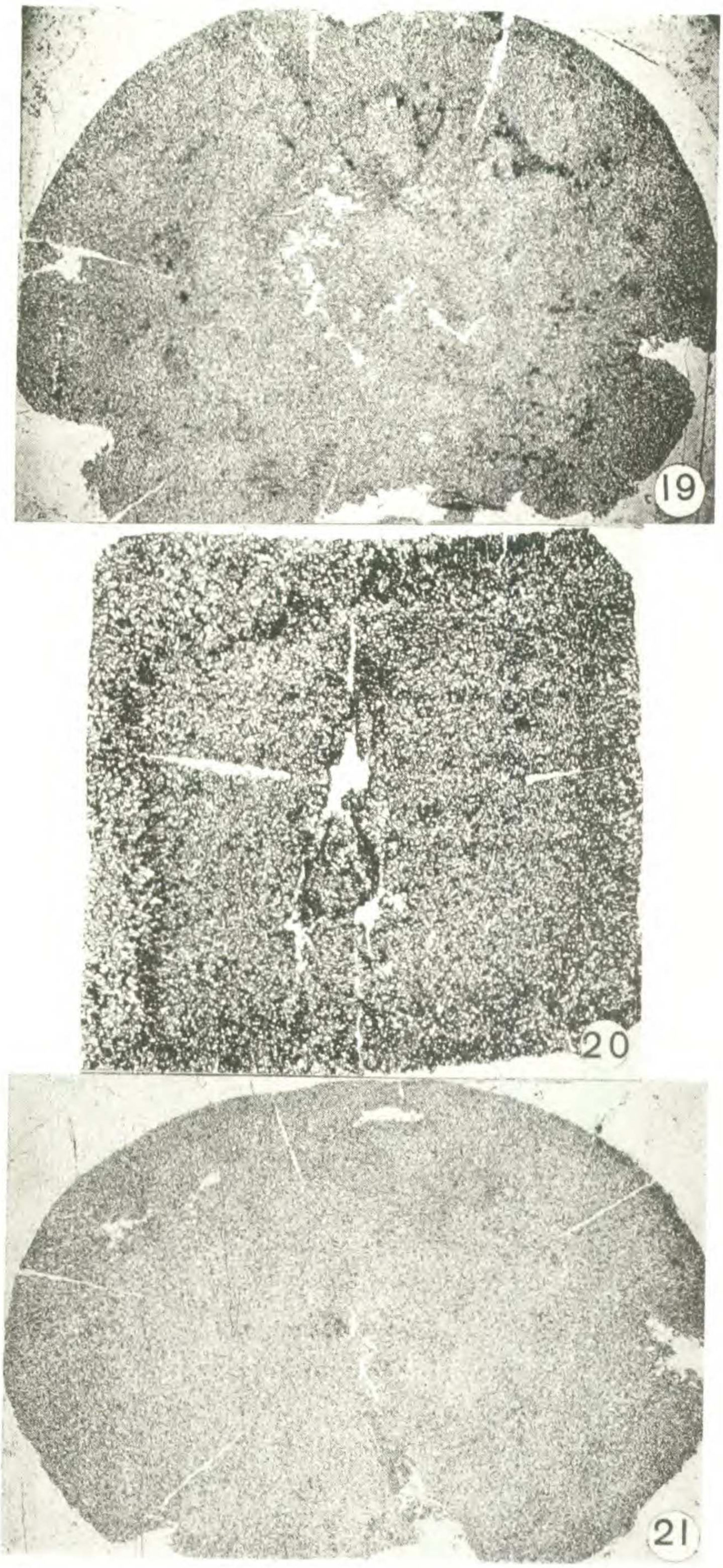

WETMORE AND S. SOROKIN, DIFFERENTIATION OF XYLEM

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VOL. XXXVI OCTOBER 1955 NUMBER 4

A MONOGRAPH OF THE GENUS PHILADELPHUS *

SHIU-YING HU

Series 5. **Delavayani**, ser. nov.

Philadelphus subg. II. **Euphiladelphus** sect. 4. **Stenostigma** ser. 5. **Delavayani**, ser. nov.

Philadelphus sect. *Stenostigma* subsect. *Satsumani* Koehne in Mitt. Deutsch. Dendr. Ges. **1904** (13): 82. 1904, pro parte.

Philadelphus sect. *Poecilostigma* subsect. *Gemmati* Koehne in Mitt. Deutsch. Dendr. Ges. **1906** (15): 51. 1906, pro parte.

TYPE SPECIES: *P. delavayi* L. Henry.

Frutex ramulis griseis, raro castaneis, cortice clauso; foliis ovatis vel ovato-lanceolatis, subtus plerumque dense pubescentibus, inflorescentiis 7-, 9-, raro 5- vel 21-floris; hypanthiis glaberrimis, saepe pruinosis, purpurescentibus; corolla disciformi vel subcampanulata, raro cruciformi; staminibus 25 usque 35, disco et stylo glabris; stigmatibus linearibus, dorsalibus; capsulis obovoideis; seminibus breviter caudatis.

Both geographically and morphologically this series is intermediate between the western Himalayan series Tomentosi and the northern Chinese series Pekinense. Members of this series occur in southwestern China between Long. 98° and 102° E. and Lat. 26° and 30° N. They are characterized by their pubescent leaves, glabrous hypanthia, green and purplish calyx, linear and abaxial stigmata and short-caudate seeds. The distribution of the species in this series is shown in map 5.

KEY TO THE SPECIES

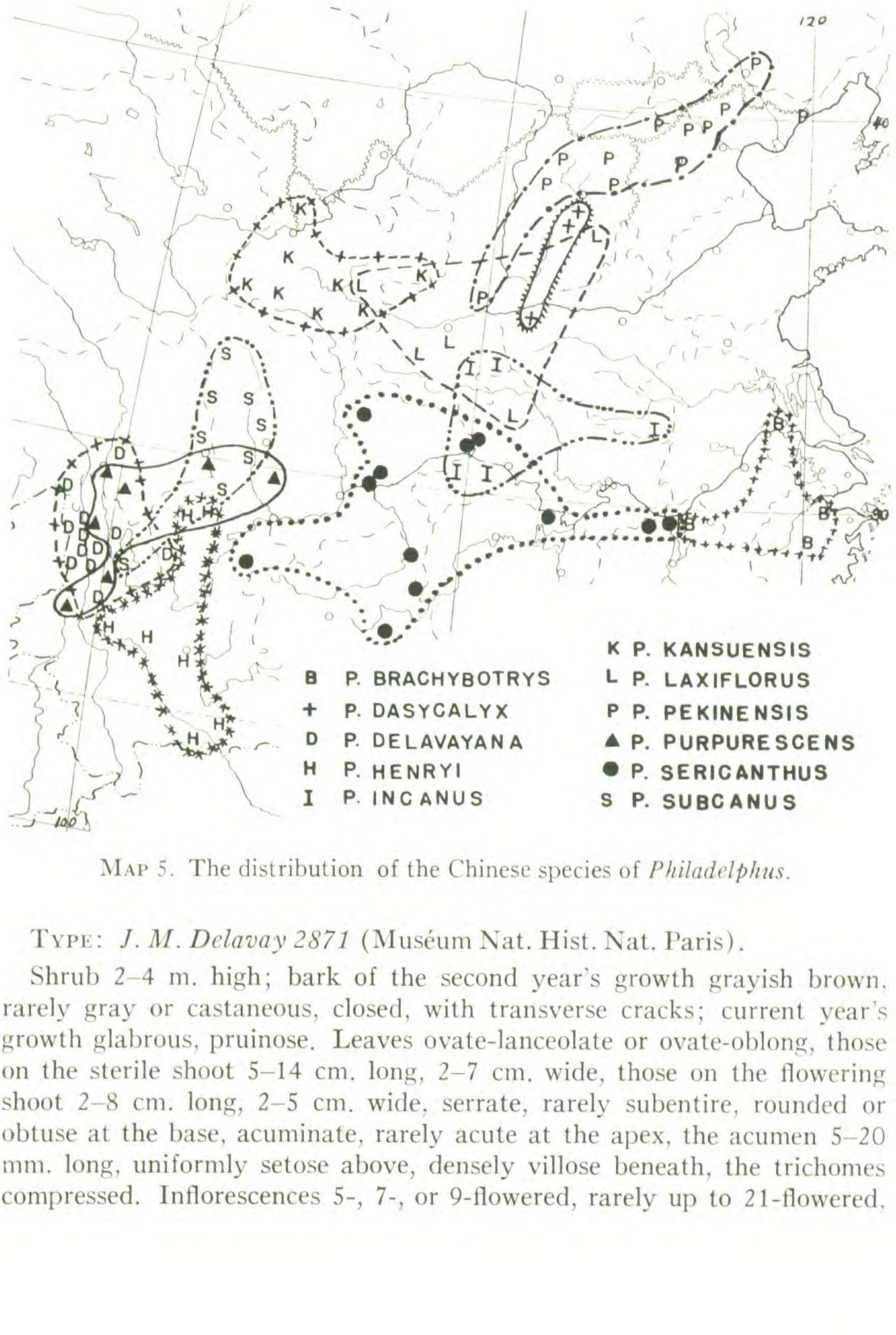
A. Hairs on the lower leaf-surface villose; corolla disciform or rarely cruciform, generally 3 cm. or more in diameter. ..... 32. *P. delavayi.*

AA. Hairs on the lower leaf-surface strigose; flowers small, the corolla campanulate, less than 3 cm. in diameter. ..... 33. *P. purpurascens.*

32. **Philadelphus delavayi** L. Henry in Rev. Hort. **1903**: 13, *fig. 3*. 1903. — Koehne in Mitt. Deutsch. Dendr. Ges. **1906**(15): 51. 1906. —

* *Continued from volume XXXVI, page 109.*

Schneider, Ill. Handb. Laubh. 1: 370. 1905. — Stapf in Bot. Mag. 149: *pl. 9022*. 1924. — Diels in Notes Bot. Gard. Edinb. 7: 106. 1912. — Léveillé, Cat. Pl. Yunnan 255. 1917. — Rehder, Man. Cult. Trees Shrubs 275. 1927; ed. 2, 269. 1940; et Bibl. Cult. Trees Shrubs 192. 1949. — Hand.-Mazz., Symb. Sin. 7: 438. 1931. — Chen, Ill. Man. Chin. Trees Shrubs 372, 1937. — Merr. in Britt. 4: 66. 1941. — Bean in Chitt., Dict. Gard. 3: 1546, *fig.* [1]. 1951.



MAP 5. The distribution of the Chinese species of *Philadelphus*.

TYPE: *J. M. Delavay 2871* (Muséum Nat. Hist. Nat. Paris).

Shrub 2–4 m. high; bark of the second year's growth grayish brown, rarely gray or castaneous, closed, with transverse cracks; current year's growth glabrous, pruinose. Leaves ovate-lanceolate or ovate-oblong, those on the sterile shoot 5–14 cm. long, 2–7 cm. wide, those on the flowering shoot 2–8 cm. long, 2–5 cm. wide, serrate, rarely subentire, rounded or obtuse at the base, acuminate, rarely acute at the apex, the acumen 5–20 mm. long, uniformly setose above, densely villose beneath, the trichomes compressed. Inflorescences 5-, 7-, or 9-flowered, rarely up to 21-flowered,